

Diatom response to climatic warming over the last 200 years: A record from Gonghai Lake, North China

Yao Yan^a, Luo Wang^{b,*}, Jie Li^a, Jingjing Li^a, Yafei Zou^{b,c}, Jiaoyang Zhang^a, Peng Li^d, Yuan Liu^d, Bing Xu^{b,c}, Zhaoyan Gu^{b,c}, Xiaoqiao Wan^a

^a State Key Laboratory of Biogeology and Environmental Geology, and School of Earth Science and Resources, China University of Geosciences, Beijing, 100083, China

^b Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, 100029, China

^c University of Chinese Academy of Sciences, Beijing, 100049, China

^d School of Earth Science and Resources, China University of Geosciences, Beijing, 100083, China

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ABSTRACT

Annual monitoring data and centennial and millennial-scale paleolimnological records have revealed an increase in small-celled planktonic diatom species relative to heavier tycho-planktonic and small benthic diatoms in many high-altitude lakes, presumably in response to recent climatic warming. In addition to changes in the composition and structure of lacustrine diatom assemblages, there have also been changes in diatom biodiversity; however, these changes are not regionally consistent. In this study, we chose a temperate mid-latitude lake to explore the response of changes in diatom assemblages and biodiversity to recent climatic warming. The diatom record spans the past ca. 200 years and reveals that since 1966 CE the small-celled *Cyclotella ocellata* + *stelligera* has replaced the previously dominant, large-celled phytoplankton *Cyclotella schroeteri*. These changes are in accordance with the increasing trend in global mean surface temperature. Biodiversity increased remarkably from 1966 CE, but began to decline after 1990 CE, presumably in response to rapid climatic warming. Our findings indicate that the response of diatom biodiversity to climate change was a nonlinear process.

1. Introduction

Climate is the main driver of ecological change and recent global warming has affected ecosystems on a global scale (Parmesan and Yohe, 2003). Diatom analysis of lake sediments is a powerful tool for assessing the effects of climate variability on lake ecosystems (Battarbee et al., 2001). Shifts in diatom assemblages often occur rapidly in response to ecological perturbations. Annual monitoring data, and centennial- and millennial-scale paleolimnological studies show that the relative abundance of the small-celled planktonic diatom *Cyclotella* taxa has increased remarkably in diatom assemblages in alpine, boreal, temperate, and arctic areas (Gerten and Adrian, 2002; Perren et al., 2003; Smol et al., 2005; Enache et al., 2011; Saros et al., 2012; Panizzo et al., 2013; Rühland et al., 2008, 2013, 2015). This change is often attributed to the direct effects of increasing temperatures on the physical structure of lakes, based on inferences from small-scale experiments and contemporary observational studies (Saros et al., 2014). However, this change is not consistent across all regions, and paleolimnological records from several regions that have experienced climatic warming show a decrease in the relative abundance of small-celled planktonic *Cyclotella* taxa in boreal, alpine, and arctic areas (Perren and

Douglas, 2009; Perren et al., 2012; Hobbs et al., 2010; Saros et al., 2011, 2012). Moreover, sometimes contrasting responses are shown by the same species in lakes no more than 3 km apart (Rühland et al., 2015).

Furthermore, many lakes were reported to be affected to varying degrees by human impacts (such as nutrient enrichment, acidification, and pollution) (Bennion et al., 2004; Bigler et al., 2007; Panizzo et al., 2013; Wischniewski et al., 2014). However, high-altitude areas tend to have relatively low levels of human impact compared to lowland areas where nutrient concentrations can increase dramatically (Lotter, 1998; Kauppi et al., 2002; Bradshaw et al., 2006; Bigler et al., 2007). Nevertheless, even remote sites have experienced human impacts, such as through the deposition of atmospherically-derived nutrients (Wolfe et al., 2001, 2003) or intensive animal husbandry (Hausmann et al., 2002). Therefore, it is a legitimate hypothesis to posit that the observed recent changes in diatom assemblages are linked to human activities.

The signals of climate change in temperate regions are often blurred due to multiple factors (Smol, 2008; Rühland et al., 2008). However, climate change has significantly affected physical, biological and chemical processes in freshwater ecosystems in remote temperate regions that are relatively undisturbed by human activity (Schindler, 1997;

* Corresponding author.

E-mail address: wangluo@mail.iggcas.ac.cn (L. Wang).

Gerten and Adrian, 2002; Rühland et al., 2008). In addition, several studies have shown that high latitudes are extremely sensitive to climate change. For example, the timing of initial increases in *Cyclotella* s.l. species in high latitude lakes have preceded similar increases in high altitude regions by about 50 years, and have preceded increases in lower latitude, temperate lakes by about 100 years (Smol et al., 2005; Smol and Douglas, 2007; Rühland et al., 2008, 2015). It is clearly important to determine if the diatom assemblages of lakes at relatively low latitudes in temperate regions have also responded to climate change.

It is known that many lake ecosystems are threatened both by human demands and climatic effects (global warming), but little is known about the possible responses of their algal biodiversity. In addition, few recent studies have been designed to investigate diatom biodiversity, and instead most have focused on the response of lake ecosystems to various drivers based on changes in the relative abundance of diatom species (Yang et al., 2002, 2004, 2008; Rioual et al., 2007; Wang et al., 2012a, 2012b). Smol et al. (2005) concluded that changes in the beta diversity of diatoms in Arctic lakes are especially pronounced in those areas which have experienced the greatest warming, whereas the smallest changes have occurred in regions that have experienced little or no recent warming within the past ca. 150 years. Similarly, at Lake Xiaolongwan in northeast China, there was an increased beta diversity with climate warming since ca. 1940 CE

the possible effect of climate change on lacustrine biodiversity.

In this study, we investigated the relationship between the diatom biodiversity of surface sediment samples and water depth in Gonghai Lake, a freshwater alpine lake on the Chinese Loess Plateau. In addition, we analyzed changes in diatom assemblages biodiversity of a sediment core from the lake over the past about 200 years.

2. Materials and methods

2.1. Study site

Gonghai Lake (38° 54'N, 112° 14'E; 1840 m above mean sea level) is located on the Chinese Loess Plateau (Fig. 1A). This remote, freshwater, high-elevation lake is hydrologically closed, with a simple basin morphometry with a flat floor, and a small, undisturbed catchment (Fig. 1C). The surface area is about 0.36 km² and the maximum water depth is about 10 m. The location and watershed characteristics of Gonghai Lake make it well-suited for monitoring environmental and climatic change. The monthly mean temperature in the region ranges between −14 °C and 23 °C, and currently the lake is typically ice-covered from the middle of November to the end of April. The vegetation in the catchment is dominated by *Hippophae rhamnoides* scrubland and *Bothriochloa ischaemum* grassland, and *Carex* spp. are common in the lake basin.

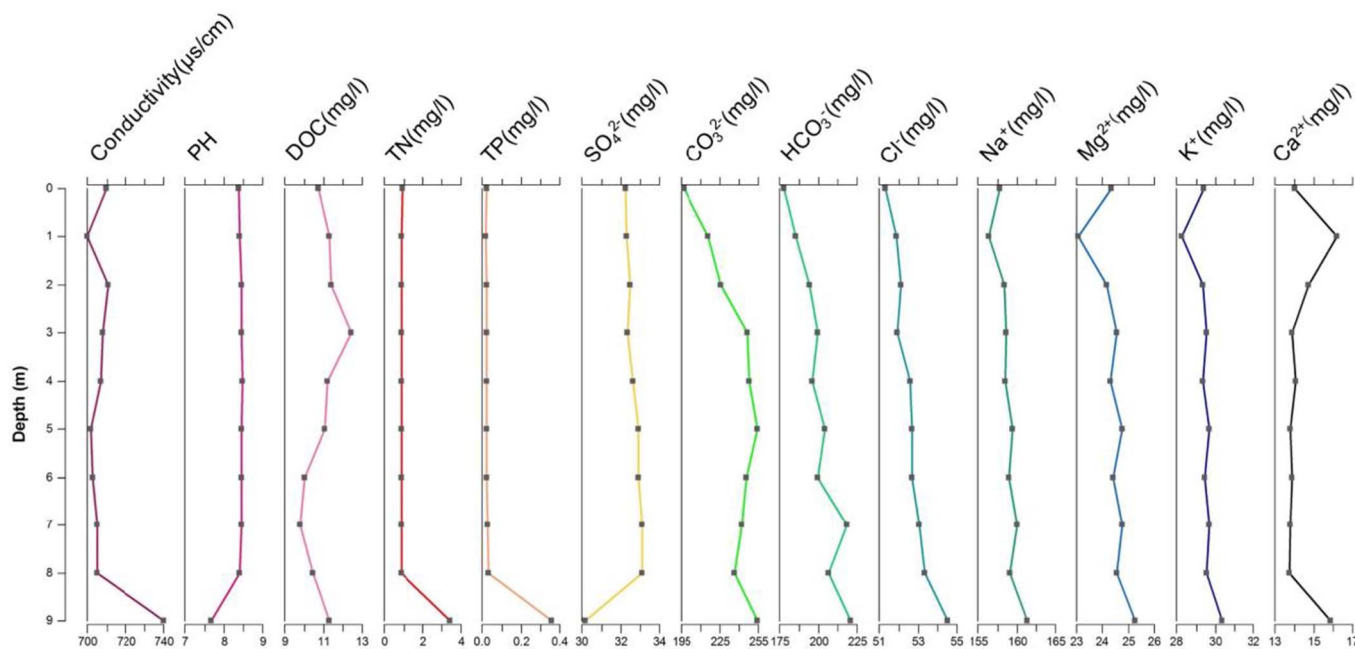


Fig. 1. Site location and setting. A. Location of Gonghai Lake in Ningwu County, Shanxi Province (green dot). B. Bathymetry of Gonghai Lake. The black dots indicate the location of the Gonghai Lake surface samples and red star indicates the location of cores GH2013A. B. C. Photograph of Gonghai Lake and its catchment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Panizzo et al., 2013). In contrast, Włodarska-Kowalczyk and Weslawski (2001) concluded from a study of two Arctic glacial bays that one of the consequences of climatic warming for Arctic ecosystems will be a decline of benthic biodiversity.

It is important to consider, however, if the biodiversity of a sample from a single location in a lake can represent the biodiversity of the entire lake ecosystem. Some studies have found pronounced differences in the biodiversity of samples from different areas and depth zones in ice-covered lakes at high latitudes (Melissa et al., 2005; Laird et al., 2010). Zou et al. (2015) demonstrated that lakes at low latitudes, such as Yunlong Tianchi, which has a relatively simple morphology and a well-mixed water column, show no pronounced differences in diatom biodiversity at different locations. Therefore, it is important to examine whether diatom biodiversity changes with water depth before assessing

Lake Gonghai is currently alkaline, with pH ranging from 7.69 to 8.48, depending on water depth, and conductivity ranges from 702 to 740 μs/cm. The concentration of dissolved organic carbon (DOC) ranges from 9.81 to 12.46 mg/l (average of 10.98 mg/l), and the concentrations of total phosphorus (TP) and total nitrogen (TN) from 0.020 to 0.360 mg/l and 0.87 to 3.41 mg/l, respectively; the lake is strongly phosphorus limited (TN:TP mass ratio = 19.2). The concentrations of HCO₃⁻, CO₃²⁻ and Na⁺ are relatively high, with average values of 200.4, 236.7 and 158.9 mg/l, respectively; and the concentrations of Ca²⁺, K⁺, Mg²⁺, Cl⁻ and SO₄²⁻ are relatively low, with average values of 14.4, 29.5, 24.4, 52.7 and 32.4 mg/l, respectively (Fig. 2; Table 1). The Gonghai Lake region has experienced a large increase in mean annual temperature in response to global warming (Wang et al., 2014; Liu et al., 2017).

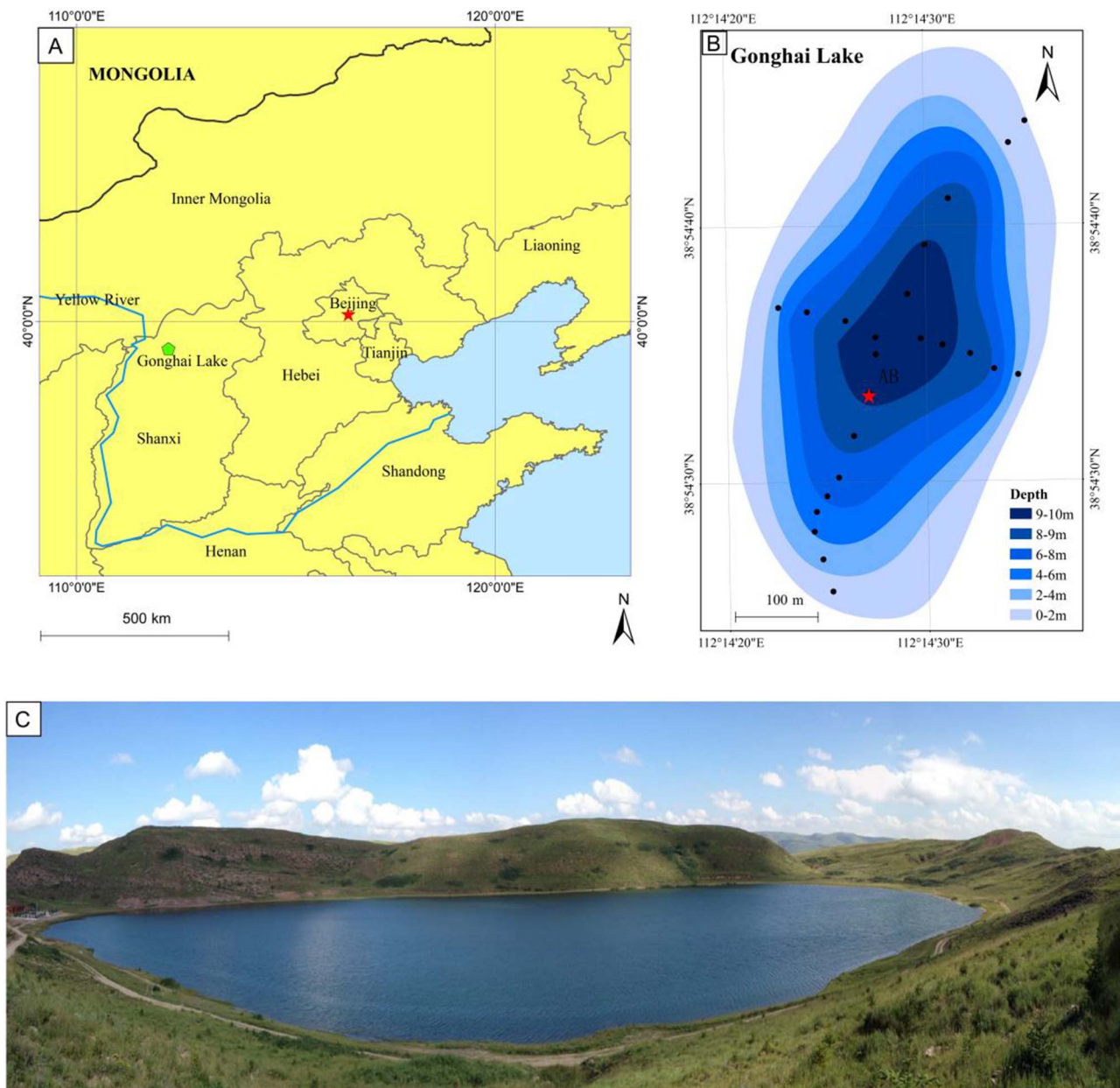


Fig. 2. Variation of the water chemistry of Lake Gonghai in relation to water depth.

Table 1
Variation of physical and chemical characteristic of Gonghai Lake with water depth.

	0 m	1 m	2 m	3 m	4 m	5 m	6 m	7 m	8 m	9 m
Conductivity (μs/cm)	710	700	711	708	707	702	703	705	705	740
PH	8.39	8.41	8.47	8.47	8.48	8.47	8.47	8.47	8.41	7.69
DOC (mg/l)	10.73	11.30	11.42	12.46	11.22	11.05	10.04	9.81	10.44	11.30
TN (mg/l)	0.939	0.890	0.873	0.906	0.881	0.911	0.891	0.890	0.900	3.412
TP (mg/l)	0.024	0.020	0.024	0.025	0.023	0.025	0.023	0.028	0.031	0.360
SO ₄ ²⁻ (mg/l)	32.24	32.32	32.50	32.35	32.66	32.94	32.91	33.12	33.13	30.19
CO ₃ ²⁻ (mg/l)	196.9	215.9	225.9	246.7	247.9	254.1	245.8	242.2	236.9	254.3
HCO ₃ ⁻ (mg/l)	178.0	185.5	194.4	199.9	196.0	204.5	199.4	218.7	206.8	221.0
Cl ⁻ (mg/l)	51.34	51.88	52.14	51.95	52.60	52.69	52.68	53.05	53.33	54.54
Na ⁺ (mg/l)	158	156	158	159	159	159	159	160	159	161
Mg ²⁺ (mg/l)	24.3	23.1	24.2	24.6	24.3	24.7	24.4	24.8	24.5	25.3
K ⁺ (mg/l)	29.4	28.3	29.3	29.5	29.4	29.7	29.5	29.7	29.6	30.3
Ca ²⁺ (mg/l)	14.0	16.2	14.7	13.9	14.1	13.8	13.9	13.8	13.8	15.9

Table 2
Names and codes of the diatom species used for principal components analysis.

Number	Species
1	<i>S.hantzschii</i>
2	<i>C.schroeteri</i>
3	<i>C.placentula</i> var. <i>lineata</i>
4	<i>N.menisculus</i>
5	<i>R.gibba</i>
6	<i>E.sorex</i>
7	<i>C.ocellata</i> + <i>stelligera</i>
8	<i>A.ohridana</i>
9	<i>C.meneghiniana</i>
10	<i>F.capucina</i> var. <i>vaucheriae</i>
11	<i>F.pulchella</i>
12	<i>D.teuis</i>
13	<i>A.minutissima</i> var. <i>Africana</i>
14	<i>A.minutissima</i> var. <i>Minutissima</i>
15	<i>A.copulate</i>
16	<i>F.capucina</i> var. <i>gracilis</i>
17	<i>F.ulua</i> var. <i>acus</i>
18	<i>N.cryptotenella</i>
19	<i>N.cf. agnita</i>
20	<i>E.microceplala</i>

2.2. Sampling design

In August 2013, three sediment cores (GH2013A-C) were obtained from the center of Gonghai Lake using a UWITEC gravity corer. In addition, 23 surface sediment samples were taken along north-south and east-west transects (Fig. 1B), also using the UWITEC gravity corer. The water depth at each sample location was measured using an echo sounder and

the location was recorded using GPS. The cores were sliced into 1 cm intervals in the field. Cores GH2013A and GH2013B were drilled from the same position but have a different diameter (Fig. 1B). Core GH2013B, used for this study, has a diameter of 6 cm and a length of 1.1 m.

2.3. Laboratory methods and chronology

The chronology of the uppermost 50 cm of core GH2013B was developed using ^{210}Pb -dating and the CRS (Constant Rate of Supply) model, together with the location of peaks in the distribution of ^{137}Cs (Krishnaswamy et al., 1971; Appleby and Oldfield, 1978). Based on this chronology the core spans the interval from 1844 CE to 2012 CE (Fig. 3).

Diatom slides were prepared using conventional methods. Approximately 0.05 g of dry sediment from each sample was heated with H_2O_2 followed by HCl to remove organic matter and carbonate, respectively (Battarbee et al., 2001; Li et al., 2009). 500 diatom valves were counted from each sample.

To evaluate the diatom diversity of Gonghai Lake, several biodiversity indices were calculated: the Margalef index, Simpson index, Pielou index, Shannon-Weiner index and PIE index. The Margalef index is based on the number of taxa and the total number of individuals and indicates the richness of the diatom assemblages (Harper, 1999). The Pielou index and Simpson index were chosen mainly to indicate species evenness (James and Rathburn, 1981; Harper, 1999). The Shannon index and PIE index are composite diversity indices which not only indicate species richness but also reflect the evenness of species distribution; thus, they are generally used to indicate the heterogeneity of the biocenosis (Simpson, 1949; Lande, 1996; Harper, 1999).

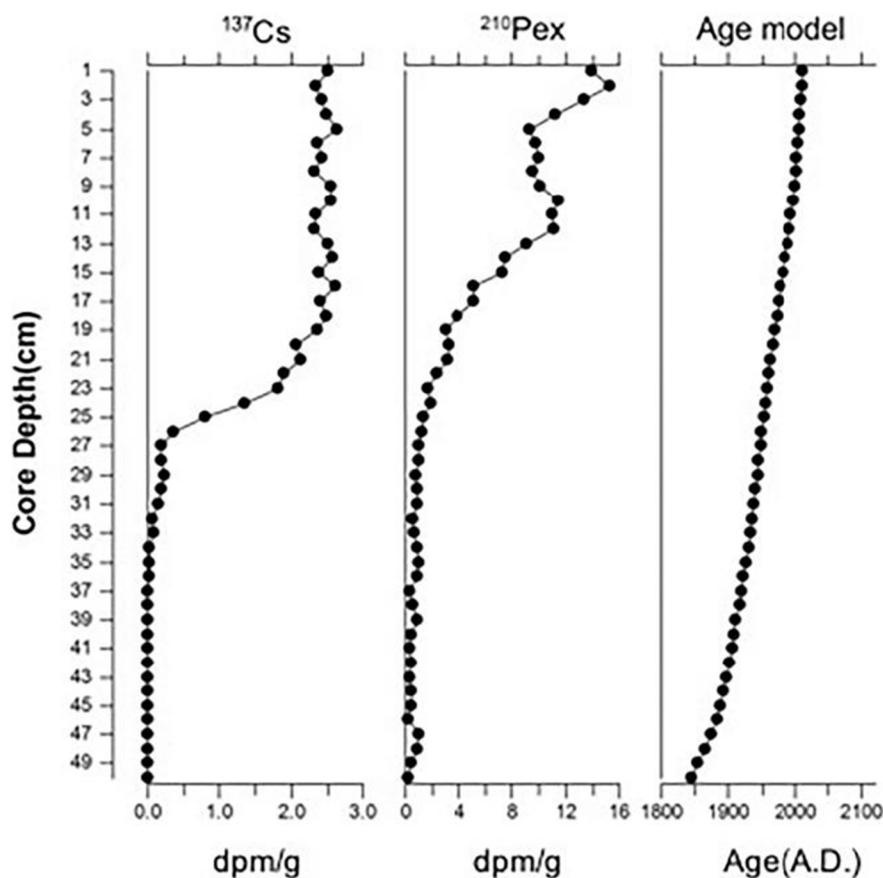


Fig. 3. ^{137}Cs and ^{210}Pb depth profiles and the age-depth model for core GH2013B.

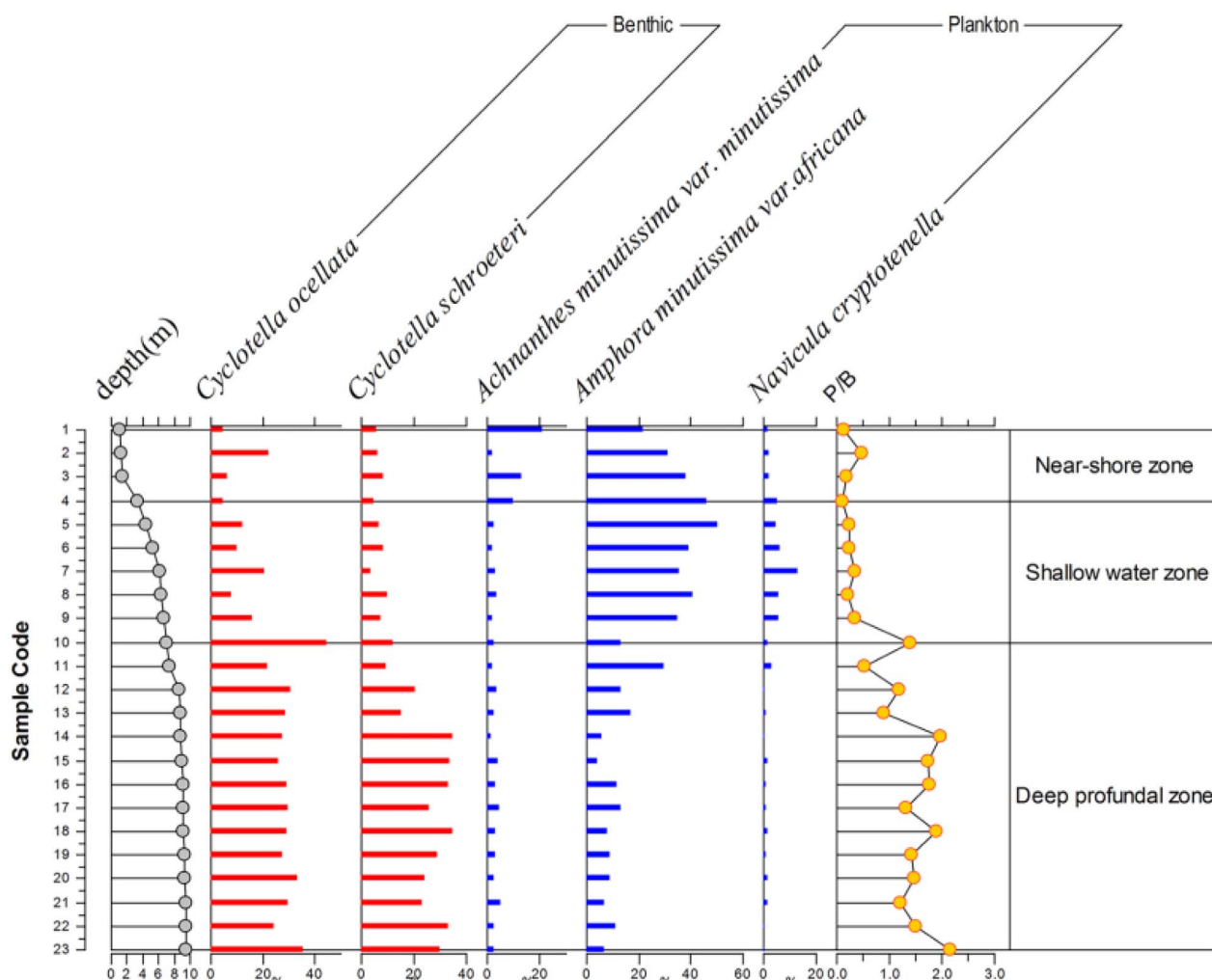


Fig. 4. Variation of the diatom composition of surface sediment samples from Gonghai Lake, in relation to water depth. P/B is the ratio of planktonic to benthic diatoms.

3. Results

3.1. Diatom assemblages and biodiversity of the surface samples

3.1.1. Diatom assemblages of surface samples

We divided Gonghai Lake into three depth zones: a near-shore zone (0–4 m), a shallow water zone (4–7 m) and a deep water profundal zone (7–10 m), and found that the diatom assemblages varied between these zones. The near-shore and shallow water zones are characterized by benthic-dominated assemblages ($P/B < 0.5$), with *A. minutissima* var. *Africana* and *A. minutissima* var. *Minutissima* as the dominant species; and the deep profundal zone is characterized by planktonic diatoms ($P/B > 1.5$), with *C. ocellata* and *C. schroeteri* as the main species (Fig. 4).

3.1.2. Diatom biodiversity of surface samples

The diatom biodiversity of the surface samples shows no obvious changes with water depth. Although the Margalef index exhibits a relatively wide range (4.01–5.72) there is no pronounced trend. The other three indices, Pielou index, the Simpson index and the Shannon-wiener index, change little with depth and fluctuate between 0.45 and 0.59, 0.72–0.88 and 1.98–2.59, respectively (Fig. 5).

3.2. Diatom assemblages and biodiversity in core GH2013B

3.2.1. Diatom assemblages in core GH2013B

The diatom assemblages in core GH2013B are dominated by

planktonic forms, with the main species being *Cyclotella ocellata*, *Cyclotella meneghiniana*, *Cyclotella stelligera*, *Cyclotella schroeteri*, and *Stephanodiscus hantzschii*. The main benthic species are *Achnanthes minutissima* var. *minutissima*, *Amphora copulate*, *Amphora minutissima* var. *Africana*, *Amphora ovalis*, *Amphora ohridana*, *Cocconeis placentula* var. *lineata*, *Diatoma teuis*, *Epithemia sorex*, *Encyonopsis microcephala*, *Fragilaria capucina* var. *gracilis*, *Fragilaria capucina* var. *vaucheriae*, *Fragilaria ulua* var. *acus*, *Navicula cryptotenella*, *Navicula menisculus*, *Nitzschia cf. agnita*, and *Rhopalodia gibba*.

The results of cluster analysis and the changes in the composition of the diatom assemblages enable the record to be divided into three zones (Fig. 6) which are described below.

Zone I (50–20 cm, 1844–1966 CE). This zone is dominated by planktonic species (68–88%), among which, *C. schroeteri* is the most common (55–87%), and *S. hantzschii* has a relatively low abundance. The benthic species *Amphora copulate*, *A. minutissima* var. *Africana*, *R. gibba* and *E. sorex*, although common, are less well represented.

Zone II (20–1 cm, 1966–2012 CE). This zone is distinguished from zone I by an increase in the abundance of the planktonic diatom *C. ocellata* + *stelligera* mixed group (3%–53%) and the benthic diatoms *A. copulate* and *A. minutissima* var. *Africana*. The planktonic diatom *C. schroeteri*, which is the most common diatom throughout the core, decreases from 55 to 3%.

3.2.2. Diatom biodiversity in core GH2013B

The changes in the diatom diversity of Gonghai Lake from 1844 CE to 2012 CE, indicated by the various biodiversity indices, are shown in

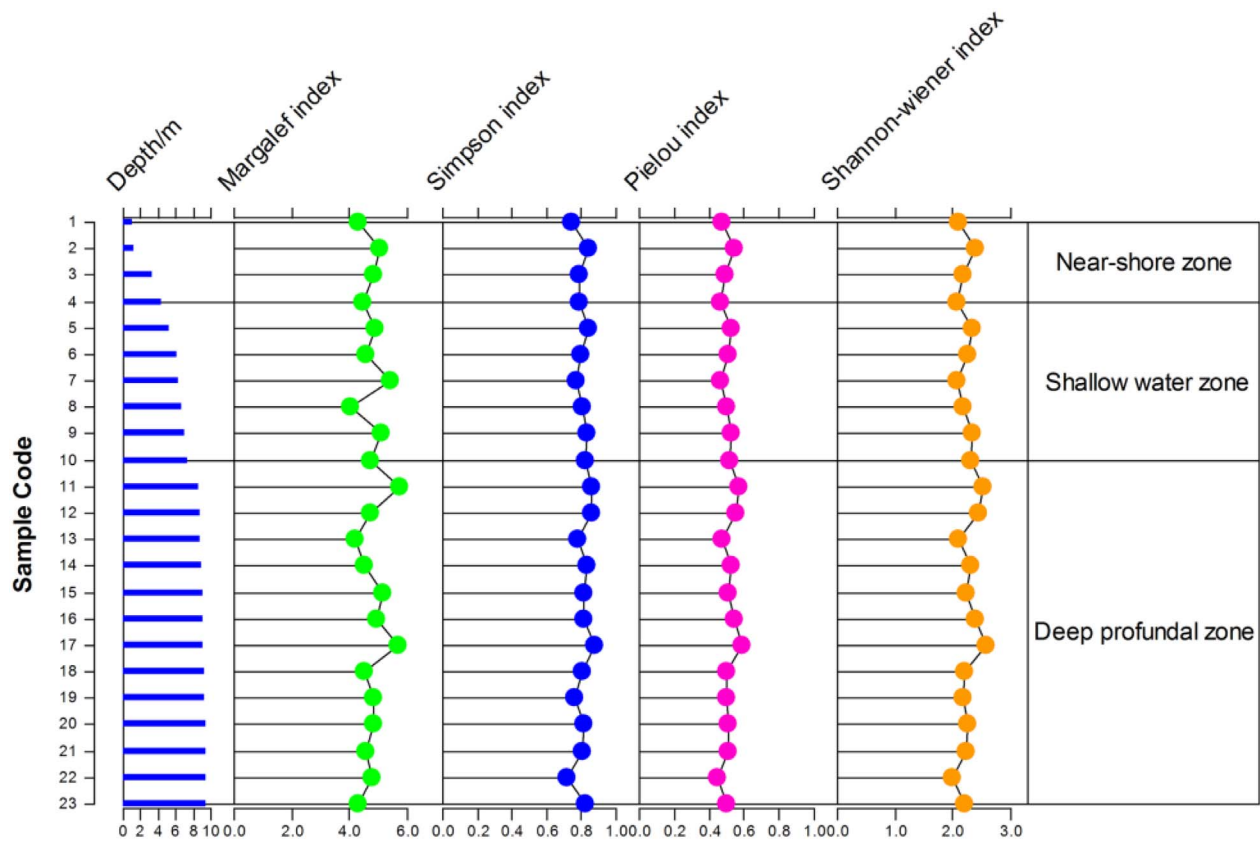


Fig. 5. Variation of the diatom biodiversity of surface sediment sediments from Gonghai Lake in relation to water depth.

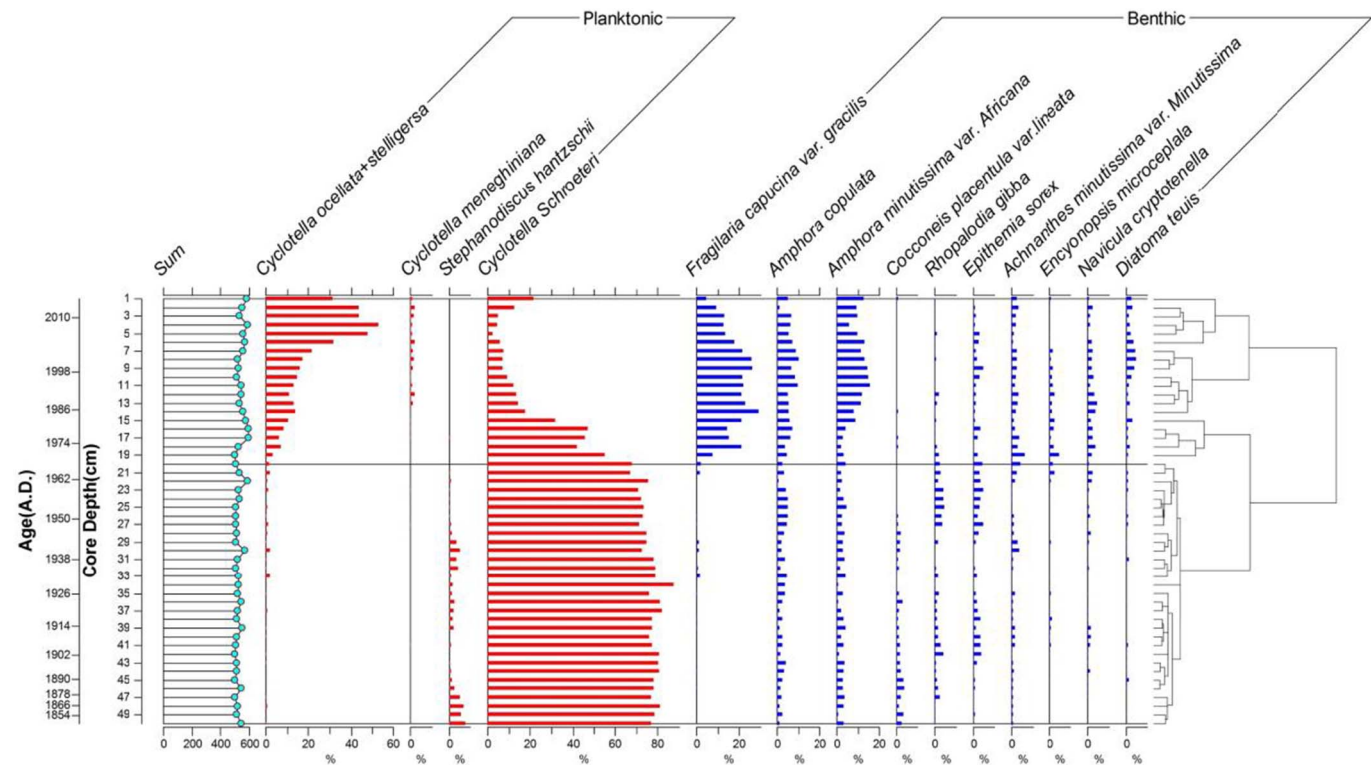


Fig. 6. Changes in the relative abundance of the most common diatom taxa in core GH2013B from Gonghai Lake. The numbers of total diatoms, planktonic diatoms and benthic diatoms are shown in green, red and blue, respectively. The percentages are based on the sum of total diatoms. The results of cluster analysis and changes in diatom composition enable the record to be divided into two zones, separated by the horizontal line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

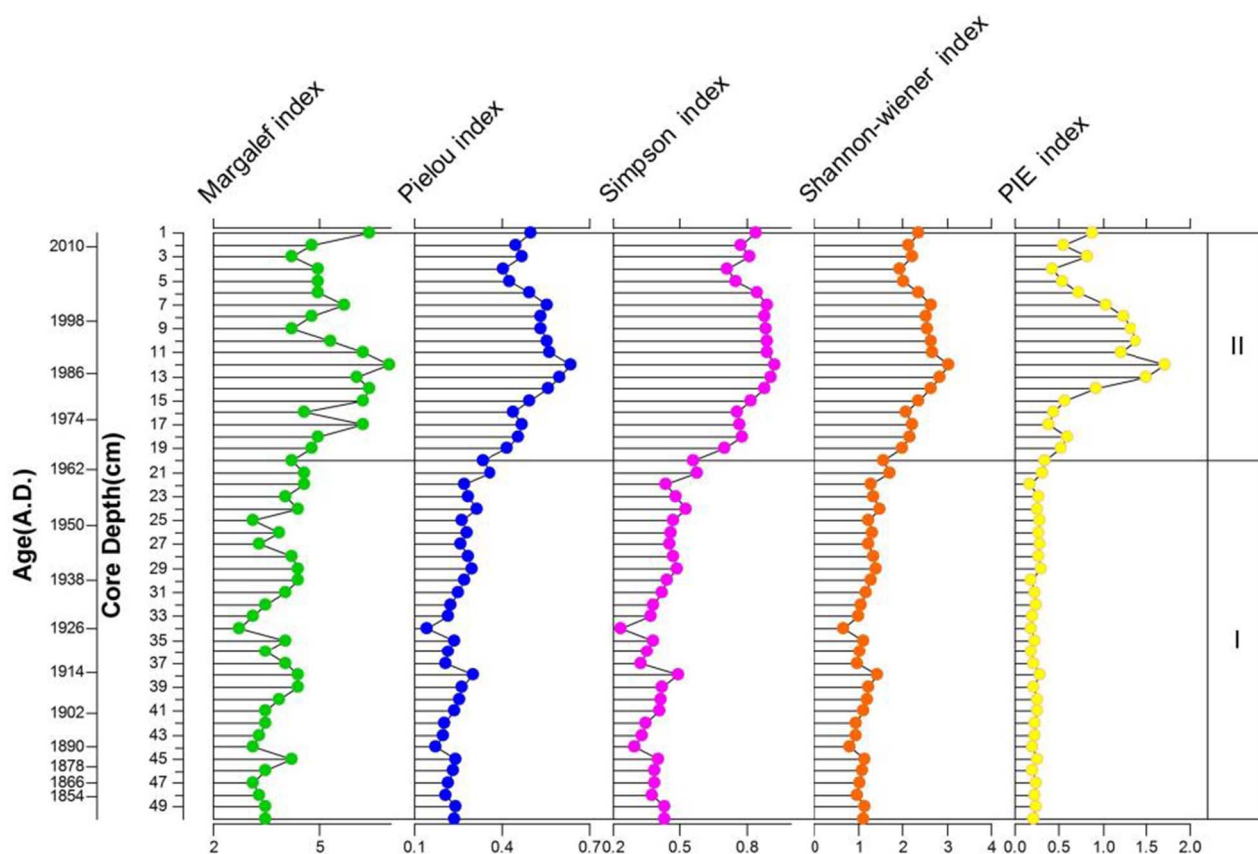


Fig. 7. Changes in diatom biodiversity in core GH2013B from Gonghai Lake. The changes in diatom biodiversity enable the record to be divided into two stages, separated by the horizontal lines.

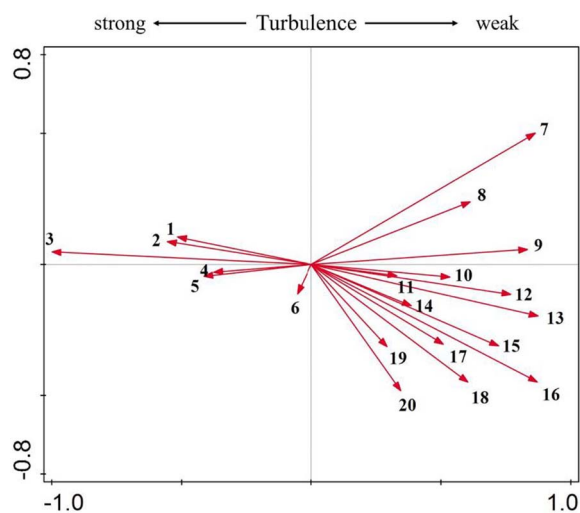


Fig. 8. Results of principal components analysis of the diatom data from core GH2013B. Numbers are species names and are listed in Table 2; the position of the arrow is determined by the regression coefficients of the standardized species data with the principal axes. The interpretation of the axes is based on the ecology of diatom species that are most strongly correlated with the axes; see text for explanation.

Fig. 7. The changes in biodiversity can be divided into two stages:

Stage I (1844–1966 CE). Diatom biodiversity was low and stable. The Margalef index varies from 2.75 to 4.58, the Pielou index from 0.14 to 0.31, the Simpson index from 0.23 to 0.53, the Shannon-wiener index from 0.98 to 1.26, and the PIE index from 0.17 to 0.30. In addition, the Margalef index exhibits a slightly higher range of change, and the other four biodiversity indices are essentially constant.

Stage II (1966–2012 CE). Diatom biodiversity changed remarkably compared to the previous stage, with an increase first, followed by a decline. The Margalef index increases from 4.22 to 6.97 and then decreases to 4.21; the Pielou evenness index increases from 0.33 to 0.64, and then decreases to 0.41; the Simpson index increases from 0.56 to 0.93, and then decreases to 0.71; the Shannon-wiener index increases from 2.29 to 4.38, and then decreases to 1.94; and the PIE index increases from 0.3 to 1.71, and then decreases to 0.42. All the biodiversity indices increase gradually from 1966 CE and then start to decrease from 1990 CE.

3.3. Principal components analysis (PCA) of the diatom assemblages

Principal components analysis (PCA) was used to summarize the diatom data for core GH2013B (Fig. 8). Only taxa with an abundance of at least 1% (20 taxa in total) were included in the analysis. The relative abundance data were square-root transformed. PCA-axis 1 explains 92.5% of the variance. *C. ocellata* + *stelligera* and *C. meneghiniana* have very high positive loadings (0.863 and 0.834, respectively) on this axis while *C. schroeteri*, *S. hantzschii* and *C. placentula* var. *lineata* have high negative loadings (−0.9996, −0.515 and −0.554, respectively). Axis-2 explains only 5% of the variance and is considered further.

4. Discussion

4.1. Representation of biodiversity of lake surface sediment samples

Some evidence suggests that diatom biodiversity changes with water depth, with the shallow near-shore zone having much higher biodiversity than the deeper zones. This is interpreted as a likely result of increased habitat diversity in the near-shore area (Caballero et al., 2002; Melissa et al., 2005; Laird et al., 2010). If the diversity of

lacustrine diatom biodiversity varies with water depth, as described above, then such lakes will be unsuitable for the study of past changes in biodiversity because the sediment samples at a specific location will not provide a good representation of the biodiversity of diatoms throughout the entire lake.

Interestingly, the lakes referenced above have the following commonalities: (1) they are all located at relatively high latitudes and thus have a long ice-cover period, which may result in poor mixing of the water column; and (2) almost all of them have a relatively complex bathymetry with a wide range of habitats in the littoral zone. Furthermore, Zou et al. (2015) studied an alpine lake, Yunlong Tianchi in Yunnan Province, which has relatively stronger vertical mixing of the water column and relatively simple morphometry, and found that the diatom biodiversity did not vary with changing water depth.

Gonghai Lake has both similarities and differences to the lakes described above. It is at a relatively high altitude with well-developed seasonality, in contrast to Yunlong Tianchi. However, like Yunlong Tianchi, it has a simple morphometry and is a closed basin. Therefore, it is important to determine if the diatom biodiversity in different zones of Gonghai Lake is also consistent.

23 surface sediment samples were collected at different depths at different locations in Gonghai Lake to determine the relationship between diatom diversity and water depth. The Margalef index, Simpson index, Pielou evenness index and Shannon-wiener index reveal no pronounced variation of diatom biodiversity with depth at different locations in the lake (Fig. 5), which indicates that a sample from any location can be used to represent the diatom biodiversity of the entire lake at a given moment in time.

The possible reasons for the minor differences in diatom biodiversity with depth in Gonghai Lake include the following: (1) Longer duration and higher magnitude of lake mixing. It is well known that the profundal zone of lakes is an unfavorable habitat for benthic diatoms. In the case of Gonghai Lake, although the profundal zone is mainly dominated by planktonic diatom species, most of the benthic species also occur in this zone, despite their relatively low abundance (Fig. 4). This situation is probably the result of the relatively strong mixing conditions, which can resuspend sediments in the littoral zone and transported them to the deep profundal zone. (2) The lake morphometry is simple. A complex morphometry and bathymetry of lakes may result in a high degree of diversity of diatom habitats, which can also promote high diatom diversity in the shallower zones (Melissa et al., 2005; Laird et al., 2010; Zou et al., 2015). The structure of Gonghai Lake is relatively simple and the depth gradient of the lake is shallow. This promotes a high degree of internal circulation and mixing of diatoms throughout the basin, so that the diversity of diatoms in the lake is constant with changing water depth.

Thus, we can conclude that in lakes with a simple morphometry and a closed basin, such as Gonghai Lake, the diatom biodiversity at a single location is representative of the entire basin. Even if such lakes are located at mid- and high- latitudes and have a period of ice cover, they are suitable for research into changing diatom biodiversity.

4.2. Diatom palaeoecology and environmental reconstruction

The earliest part of the diatom record from Gonghai Lake is dominated by *C. schroeteri* (Fig. 6); however, this species is not often discussed in previous studies. There is evidence that certain taxa with similar cell diameters may be functionally similar (e.g., *C. stelligera* and *C. glomerata*; Reynolds et al., 2002); therefore, taxonomic revisions of *C. schroeteri* have been transferred to the closely related species *C. compta* and *C. radiosa* which have similar cell diameters (15–40 µm). These *Cyclotella* species are fairly large in size with a relatively low surface area to volume ratio that promotes high sinking velocities (Diehl, 2002; Diehl et al., 2002; Ptacnik et al., 2003; Reynolds, 2006). They are also regarded as an indicator of changes in the physical structure of the water column (Rimet et al., 2009; Saros et al., 2012; Rühland et al.,

2015). However, there is still a relatively low abundance of eutrophic species in *C. schroeteri*-dominated assemblages, such as the planktonic diatom *S. hantzschii* and the benthic diatoms *A. copulata* and *C. placentula* var. *lineata*. In addition, large diatoms require more nutrients to survive compared to small diatoms. Therefore, it can be inferred that Gonghai Lake experienced stronger vertical mixing of the water column and relatively high nutrient enrichment between 1844 CE and 1966 CE, based on the occurrence of the *C. schroeteri*-dominated assemblages.

C. ocellata often co-occurs with *C. stelligera* and they are often considered to have similar environmental preferences. These small species have been found to have high growth rates, low nutrient requirements and a low sinking velocity (a high surface area/volume ratio (SA/V)), which provide a competitive advantage under prolonged periods of water stratification (Winder et al., 2009; Wang et al., 2012a, 2012b; Rühland et al., 2015). Therefore, in the present study we believe that the two species have similar ecological responses and thus they are combined in a mixed group.

There is an abrupt shift in diatom composition from the heavier *C. schroeteri*-dominated assemblages to the small-sized *C. ocellata* + *stelligera*-dominated assemblage after 1966, as well as increases in the complexity and diversity of benthic diatom assemblages. The trophic status of *C. ocellata* and *C. stelligera* is relatively ambiguous (Baier et al., 2004), and they are observed in oligotrophic (Moser and Kimball, 2009), mesotrophic (Rojo et al., 1999), and even eutrophic lakes (Schlegel and Scheffler, 2015). However, monitoring studies on seasonal- to decadal-scales, including those using sediment traps, water column sampling and sediment analysis, suggest that their presence may be indicative of strong water stratification during late spring and early summer (Forsström et al., 2005; Wang et al., 2012b; Wiltse et al., 2016). Therefore, the shift from large-sized *C. schroeteri*-dominated assemblages to small-sized *C. ocellata* + *stelligera*-dominated assemblages is associated with warming-induced increases in thermal stratification (Bopp et al., 2007; Falkowski and Oliver, 2007; Rühland et al., 2008, 2015; Wang et al., 2012a, 2012b). In addition, the appearance of epiphytic diatoms (e.g., *A. minutissima* var. *minutissima*, *R. abbreviate*, and *N. cryptotenella*) after 1966 may be related to the development of littoral, mossy and macrophytic substrates that are consistent with warming-induced habitat expansion (Douglas et al., 1994; Smol et al., 2005; Douglas and Smol, 2010; Beauger et al., 2015). Moreover, the decrease in the relative abundance of eutrophic diatoms may indicate reduced nutrient levels in Gonghai Lake. Therefore, compared to Zone I, it can be inferred that between 1966 CE and 201 CE Gonghai Lake was characterized by periods of weak vertical mixing of the water column, diverse habitats, and relatively low nutrient levels, based on the dominance of small-sized *C. ocellata* + *stelligera* and more complex epiphytic diatom-dominated assemblages.

4.3. Response of diatom assemblages and diatom biodiversity to climate change

Currently, there are two main views regarding the cause of recent shifts in the composition of diatom assemblages in lakes. One view is that the lengthening of the ice-free period, a reduction in vertical mixing, and enhancement of thermal stratification caused by climatic warming are the most important cause (Smol et al., 2005; Rühland et al., 2008; Wang et al., 2012a, 2012b; Panizzo et al., 2013). The other view is that lake eutrophication is the major cause of recent changes in the diatom assemblages of alpine lakes (Wolfe et al., 2003; Saros et al., 2005; Hobbs et al., 2010; Saros et al., 2011; Hundey et al., 2014).

The diatom record of Gonghai Lake for the past 2000 years indicates that the lake experienced significant natural eutrophication during the Sui-Tang Warm Period (STWP, 541–760 CE) and the Medieval Warm Period (MWP, 931–1320 CE) (Liu et al., 2017). This may have been caused by a strong summer monsoon and increased rainfall intensity that resulted in the transport of large quantities of phosphorus-rich soil

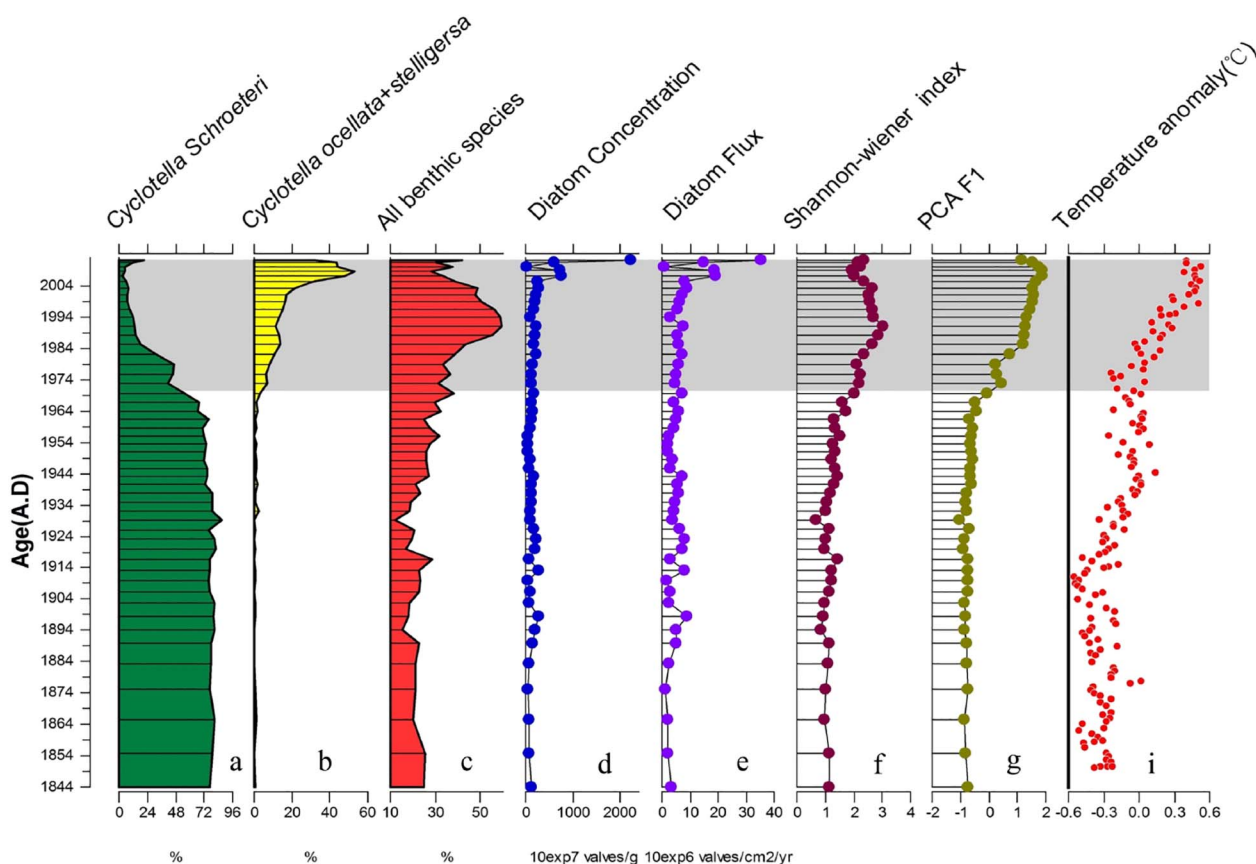


Fig. 9. Comparison of the diatom record of Gonghai Lake with temperature data. a. Relative abundance of *C. schroeteri*; b. relative abundance of *C. ocellata* + *stelligera*; c. relative abundance of all benthic species; d. diatom concentration; e. diatom flux; f. Shannon-Wiener index (the five biodiversity indexes show a similar trend and thus we use the Shannon-Wiener index as the representative); g. sample scores on PCA axis-1; h. global mean surface temperature record (IPCC, 2013). Global mean surface temperature change is strongly correlated with the temperature change over the past 55 years observed at the meteorological station in the Gonghai Lake region (Liu et al., 2017). The shaded area represents a pronounced increase in air temperature since 1966 CE.

from the catchment to the lake (Liu et al., 2017). However, weak Asian summer monsoon rainfall and wind intensity resulted in a pronounced decrease in the delivery of phosphorus-rich soil over the past few decades (Liu et al., 2017), and thus the nutrient status of Gonghai Lake has been decreasing compared to the STWP and MWP. However, the nutrient status of the lake is still relatively high, because eutrophic diatoms have been present for several hundred years and several eutrophic benthic species have appeared since about 1966, which may be related to eutrophication resulting from human activities.

Although the presence of eutrophic diatoms in Gonghai Lake may be related to human activities, the changes in diatom size show that the diatom record also documents the response of a relatively eutrophic lake to recent global changes. The eutrophic species *C. meneghiniana* first appeared in 1986 CE (maximum abundance of 2.1% and mean abundance of 0.4%). However, it is not the first nutrient-tolerant species to appear in the diatom record of Gonghai Lake: the nutrient-tolerant species *S. hantzschii* and *C. placentula* var. *lineata* occur in the beginning and middle of the record. The presence of these eutrophic species indicates that the nutrient status of Gonghai Lake has been relatively high for almost 200 years. The shift between *S. hantzschii*, *C. placentula* var. *lineata* and *C. meneghiniana* can be related to the vertical mixing of the water column, because *C. meneghiniana* in Gonghai Lake has a relatively small cell size that ranges from 50 to 15 μm in diameter, while the cells of *S. hantzschii* and *C. placentula* var. *lineata* are relatively large with a range of 15–40 μm in diameter. This is not the only response to lake hydrodynamic changes. As noted previously, the shift from large-sized *C. schroeteri* towards small-sized *C. ocellata* + *stelligera* (whose relative abundance has increased from 1.6 to 53% since 1966 CE) may be related to decreased vertical mixing. Warming-related

changes in water column properties (e.g., increased thermal stability, decreased turbulence, and nutrient distributions) tend to favor smaller-celled planktonic diatoms over heavier diatoms that require strong vertical mixing to maintain their location within the photic zone (Rühland et al., 2015).

PCA axis 1 appears to represent a gradient of water column stratification/mixing that explains 92.5% of the variance of the diatom assemblages of Gonghai Lake (Fig. 8). *C. meneghiniana* and *S. hantzschii* are often associated with eutrophic conditions; however, these two species, reflecting a similar trophic status, have very high positive (0.834) and negative loadings (−0.515), respectively. Therefore, PCA-axis 1 represents a gradient of water column stratification/mixing rather than nutrient availability because small-sized diatoms such as *C. ocellata* + *stelligera* and *C. meneghiniana* have very high positive loadings on PCA-axis 1 while larger-sized diatoms such as *C. schroeteri* and *S. hantzschii* have strong negative loadings. Furthermore, the variation of samples scores on PCA-axis 1 are highly consistent with changes in global mean temperature (Fig. 9).

The relative abundance of many benthic diatoms started to increase since 1966. Among them, *F. capucina* var. *gracilis* and *A. minutissima* var. *Africana* clearly increased, while *A. copulate*, *A. minutissima* var. *minutissima*, *R. abbreviate*, *N. cryptotenella*, *F. capucina* var. *vaucheriae*, and *F. ulua* var. *acus* increased slightly. These species represent different trophic statuses: *A. copulate* and *F. capucina* var. *gracilis* are meso-trophic-eutrophic species while *A. minutissima* var. *Africana* is oligo-trophic. Therefore, the increase in benthic diatoms cannot simply be considered to reflect increased nutrient availability. Furthermore, most of the epiphytic species are insensitive to changes in nutrient status, because they are mainly affected by macrophytes that provide more

nutrition than the water column (Lorch and Ottow, 1986; Kang et al., 2017). The development of aquatic macrophytes on a predominantly rock substrate, closely associated with climatic warming, has been observed to cause an increase in epiphytic diatoms (Barko et al., 1982; Beauger et al., 2015).

However, none of the above factors obscures the clear response of the diatom record of Gonghai Lake to recent climate change. The pronounced increase in small-sized *C. ocellata* + *stelligera* taxa and appearance of more complex benthic diatom assemblages at the expense of large-sized *C. schroeteri* taxa, in the last few decades, is a clear response to climatic warming which is directly linked to an extension of the open water period and associated changes in lake thermal properties.

The diatom assemblages in Gonghai Lake have changed remarkably over the last few decades (Fig. 6). Between 1844 and 1966, when temperature was relatively low and uniform, the diatom assemblage was simple and consisted of a few large-sized species. In addition, diatom biodiversity, in terms of species number and homogeneity, was at a relatively low level (Figs. 7, 9). It can be inferred that this status corresponded to extended periods of weak thermal stratification and low temperatures, which are associated with low abundance and diversity of diatoms. *C. schroeteri* completely dominated the assemblages during this stage because of climate-induced water column conditions and in general the diatom biodiversity remained relatively low.

There was an abrupt shift from large-sized *C. schroeteri*-dominated to small-sized *C. ocellata* + *stelligera* dominated diatom assemblages at the beginning of major industrial development in China, together with the onset of a pronounced warming trend since 1966 CE (Fig. 9). However, the change in diatom biodiversity was not linear; initially, before 1990 CE, diatom biodiversity increased together with the gradual increase in temperature (Fig. 9). During this stage, diatom species adapted to warm water temperatures began to increase and those adapted to cold water temperatures began to decrease. *C. schroeteri*, which previously was completely dominant, began to decline, while *C. ocellata* + *stelligera* and several benthic species such as *F. capucina* var. *capucina* began to increase (Fig. 6). The increase in benthic diatoms was probably the result of the increased growth of aquatic plants in littoral areas. Before 1990 CE, evidently, there was considerable competition between diatom species and none occupied a position of absolute dominance. Therefore, the number of diatoms and the diatom biodiversity increased, in parallel with the rising temperatures (Fig. 9). However, diatom biodiversity started to decrease with an interval of continuous and rapid global climatic warming since 1990 CE (Fig. 9). This may be because *C. ocellata* + *C. stelligera* occupied the dominant position within the diatom community in response to rapid warming (Fig. 6), and a phase commenced which was characterized by a high level of ecological domination, low homogeneity and decreasing diatom biodiversity.

In conclusion, shifts in *C. schroeteri*-*C. ocellata* + *stelligera*, as well as increases in the complexity and diversity of benthic diatom assemblages in Gonghai Lake, are strongly related to climate-mediated variables such as thermal stratification and vertical mixing regimes, and the availability of resources. Although diatom biodiversity also responded sensitively to climatic warming, it is important to note that the change in biodiversity was not a simple linear function.

4.4. Relationship of the sensitivity of the climatic response of diatoms to latitude and altitude

The impacts of recent climatic trends on the ecosystems of temperate latitudes are not always evident, mainly because these regions are typically subjected to multiple environmental stressors that can obscure the response to climate change (Smol, 2008; Rühland et al., 2008). However, although the nature, extent and duration of the response in different lakes varies from region to region, a response does exist (Keller, 2007; Rühland et al., 2008). For example, Rühland et al. (2008)

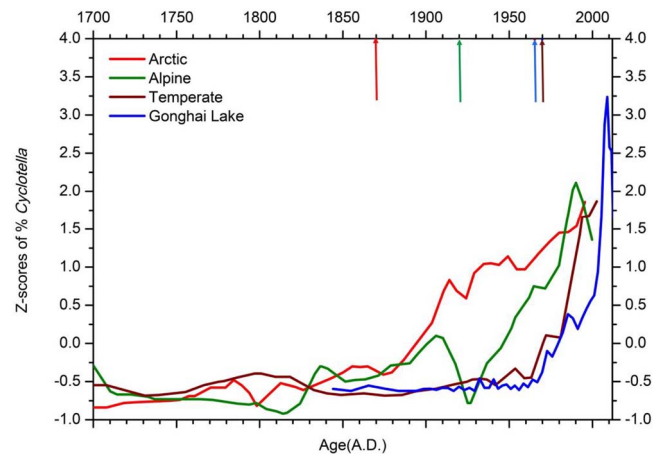


Fig. 10. Comparison of changes in the relative abundance of the small-celled planktonic diatom *Cyclotella* species in various regions of the Northern Hemisphere, compared with the record from Gonghai Lake. Arrows indicate the timing of the median abundance of *Cyclotella* species at each location (estimated from Rühland et al., 2008), compared with Gonghai Lake. Modified from Rühland et al. (2015).

found a surprisingly consistent change in diatom assemblages in different ecosystems of the Northern Hemisphere, based on diatom records from more than 200 lakes, despite the varying extent and duration of the response to climatic warming. The first pronounced increase in *Cyclotella* species, which are small and medium-celled planktonic diatoms, was about 50 years earlier at high latitudes than at high altitudes (Rühland et al., 2008, 2015). Compared to the lakes in the Arctic Circle, temperate lakes at lower latitudes experience a longer ice-free period and growing season, and will require larger and more extreme changes in climate, or a longer time interval, to exceed ecological thresholds (Rühland et al., 2008, 2015). Consequently, the shift in high latitude lakes substantially preceded that at lower latitude temperate lakes by about 100 years (Fig. 10) (Smol et al., 2005; Smol and Douglas, 2007; Rühland et al., 2008, 2015).

Rühland et al. (2015) found that the first pronounced increase in the relative abundance of the small planktonic diatom *Cyclotella* species in temperate regions occurred from about 1970 CE (Fig. 9). Gonghai Lake is in a temperate region but at a relatively high altitude (1800 m). Since 1966 CE, the major change in diatom assemblages has consisted mainly of a shift from the large-celled planktonic diatom *C. schroeteri* to the small-celled planktonic diatoms *C. stelligera* and *C. ocellata* (Figs. 5, 10), as was also noted in a study by Rühland et al. (2015).

5. Conclusions

Our results indicate that recent climatic warming has had a pronounced effect on the composition of the diatom assemblages of Gonghai Lake. Since 1966 CE, there has been a shift from large-celled diatoms to small-celled diatoms, together with an increase in the relative abundance of benthic diatoms. These changes are likely to be a response to climatic warming. The changes observed at Gonghai Lake are consistent with recent increases in the representation of small-celled planktonic diatoms in circumpolar lakes, high elevation lakes and non-acidified, non-eutrophic temperate lakes of the Northern Hemisphere. Furthermore, the increase in the representation of small-celled diatoms in the diatom assemblages of Gonghai Lake became more pronounced with the rapid warming since 1966 CE, resulting in diatom assemblages with reduced evenness and biodiversity since 1990 CE. Our results suggest that the relationship between lacustrine diatom biodiversity and increasing temperature is not a simple linear response and it is possible that the response of lacustrine diatoms to ongoing global warming may vary between different regions and environmental conditions.

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